

# The cave-dwelling dipluran (Diplura, Campodeidae) on the edge of the Last Glacial Maximum in Vancouver Island caves, North America (Canada)

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## Abstract

A new cave-dwelling dipluran of the North American endemic genus *Haplocampa* is described, coming from a couple of caves excavated in a small limestone karstic area near Port Alberni, Vancouver Island (British Columbia, Canada). To *Haplocampa* belong five soil-dwelling species. L. M. Ferguson cited no less than eight more species living in soil and cave habitats in several US states but without producing any formal descriptions. *Haplocampa*, in spite of its large lateral crests on the unequal claws, has clear taxonomical features as a Campodeinae and is closely related with the cave-dwelling *Pacificampa* and *Eumesocampa* genera, due to sharing similar macrosetae body distribution and absence or reduction of the lateral process. The new proposed species, *Haplocampa wagnelli* Sendra, **sp. n.**, is rather interesting for its troglomorphic features: antennae with 32 antennomeres; olfactory chemoreceptors, each a multiperforated, folded-spiral structure; and numerous gouge sensilla. In addition, it is one of the northernmost troglomorphic species to have colonised – presumably recently – an area occupied by the Late Wisconsinian North America ice sheet during the Last Glacial Maximum. Furthermore, the close affinities between *Haplocampa*, *Pacificampa* (from caves in the extreme east of continental Asia and the southern Japanese Islands), *Metriocampa* (from the east of Asia and North America) and *Eumesocampa* (endemic to North America) suggest probable dispersal events over the Bering Land Bridge.

**Keywords**

*Haplocampa wagnelli*, cave fauna, troglomorphic, biogeography, glaciation

**Introduction**

Although subterranean diplurans were already known from North America since the 19th century (Packard 1871), few species have been described (Condé 1949; Condé and Bareth 1996; Ferguson 1996; Sendra et al. 2016; Wygodzinsky 1944) and many remain undescribed despite a vast sampling effort. *Haplocampa* genus is a clear example. *Haplocampa* is endemic to North America (Silvestri 1911); it was first discovered in Shasta Springs, California, with its type species *Haplocampa wheeleri* Silvestri, 1911. Later, the same entomologist (Silvestri 1933) described three new species: *Haplocampa rugglesi* Silvestri, 1933; *Haplocampa chapmani* Silvestri, 1933; and *Haplocampa drakei* Silvestri, 1933. One more species of this genus could be included if we consider the form *Haplocampa* cf. *chapmani* by Condé and Geeraert (1962). These five species live in soil habitats and are distributed in Montana, Oregon and Washington in the USA and Alberta in Canada. During the 1980s and 1990s, a large sampling effort was carried out in 281 caves in California alone (Elliott et al. 2017) revealing 3 or more species of *Haplocampa*, and Ferguson (1981, 1992) reported on 7 or 8 species of *Haplocampa* from 21 lava tubes mainly in the Pacific Northwest. Ferguson (2009) also reported on his identification of 9 new species of *Haplocampa* from the caves of Colorado, bringing the total number of identified species of *Haplocampa* from caves to 26. Nevertheless, no formal description was made until now and many *Haplocampa* specimens remain undescribed in American museums and invertebrate collections (Graening et al. 2014). In 1996, the Central Island Caving Club started wandering the steep forested slopes of Vancouver Island. Since that time, the Club has mapped over 20 new caves, including what is now the most popular recreational cave on Vancouver Island. Thanks to the Club's great work, the explorations of a group of cavers from Vancouver Island (British Columbia, Canada) have given us the opportunity to describe the next new species of *Haplocampa* after more than half a century.

**Materials and methods****Sampling methods**

Fauna collections were carried out in two sites of Fossli Slot #2 and one site from Kiku Pot (see below the description of caves). Sampling was focused on regions where visible signs of chewed-up organic matter could be seen. Collections were made manually using #00 brushes and kept in small vials with 90% ethanol. Once the specimens were spotted, they were dabbed with a brush moistened with ethanol and immediately placed into vials, labelled and sealed for transport.

## Material processing and identification

The specimens were washed using distilled water and were put between slides and glass coverslips to be examined under a phase-contrast optical microscope (Leica DMLS) using Marc André II solution. The illustrations were made with a drawing tube and the measurements were taken with an ocular micrometre. For measuring the body length, the specimens were mounted 'in toto' and were measured from the base of the frontal process distal macrochaetae to the abdomen's supra-anal valve. Two paratypes were coated with palladium-gold used for scanning electronic microscopic photography (Hitachi S-4100) and measurement of the sensilla.

The morphological descriptions and abbreviations used in this article follow Condé (1956). We use gouge sensilla for the concavo-convexly shaped sensilla located on the antennae and described by Bareth and Condé (1981), the function of which is still unknown, and rosette gland formations for the epicuticular glands described in several Campodeinae species (Bareth and Juberthie-Jupeau 1996).

## Results

### *Haplocampa wagnelli* Sendra, sp. n.

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Figs 1–27; Tables 1, 2; Suppl. material 1

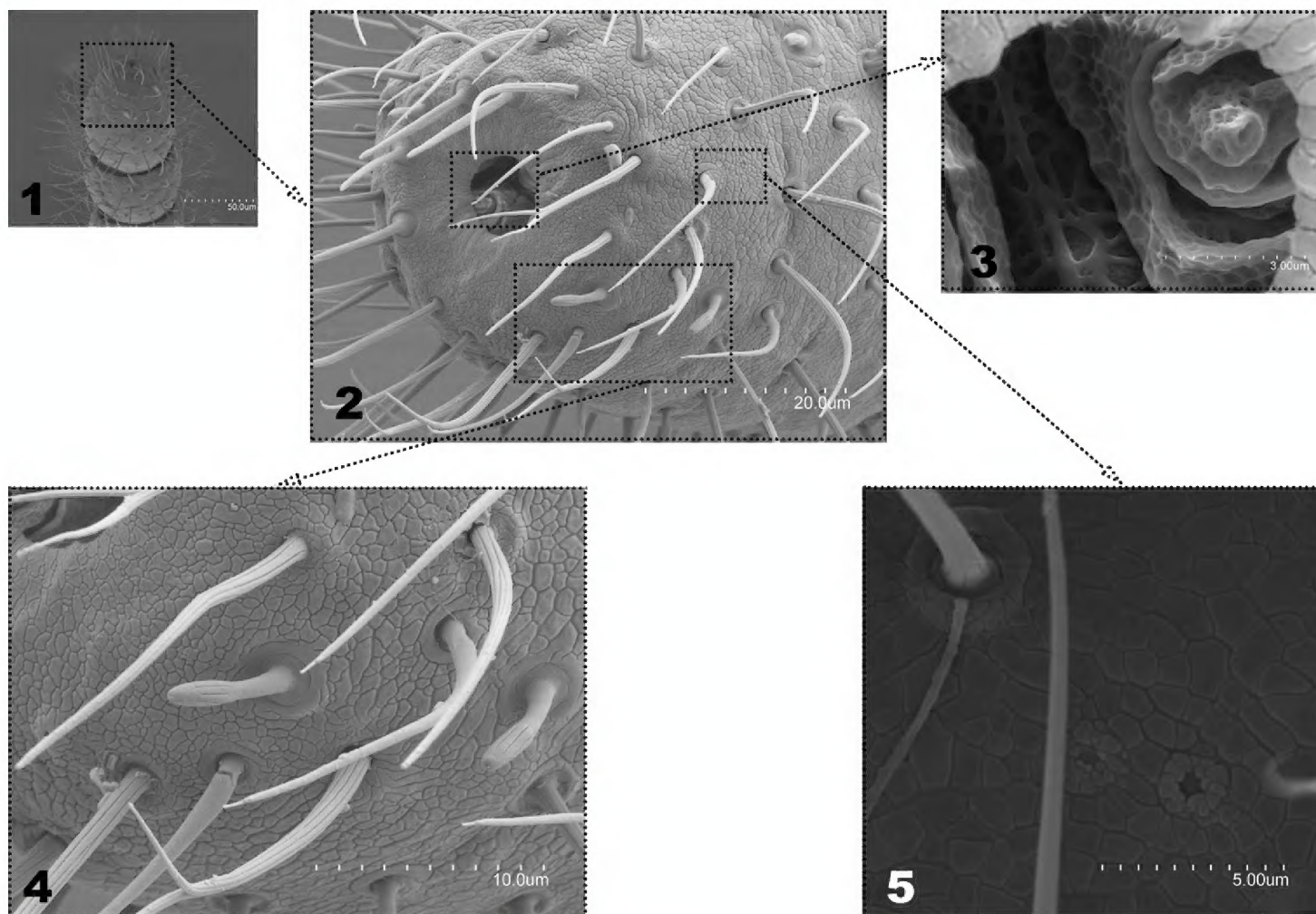
**Etymology.** This species is dedicated to the co-author of this article, a caver who has dedicated many years sampling and exploring in Vancouver Island caves.

**Type material.** Female holotype labeled ♀01 from Kiku Pot Cave, Port Alberni, Vancouver Island, Canada, 5<sup>th</sup> August 2018, C. Wagnell leg. (SEHU); 1 ♂ labeled ♂01, paratypes from Fossli Slots Caves, Port Alberni, Vancouver Island, Canada and 4 females labeled ♀02–♀05 from Fossli Slots Caves, Vancouver Island Canada, 15<sup>th</sup> July 2018, C. Wagnell leg. All type material mounted in Marc André solution. Deposited in AS collection.

**Other studied material.** Four specimens from Fossli Slots Caves, 8<sup>th</sup> June 2018, C. Wagnell leg as type material mounted in separated aluminum stages and coated with palladium-gold. Deposited AS collection.

**Description.** Body length 4.4 mm (male) and 3.4–6.0 mm (females). Epicuticle smooth under optical microscope but reticulated in high magnifications in round polygonal structures variable in size (Figs 4, 14–15); *rosette* gland formations present along the body (Figs 5, 16); body with abundant short and smooth clothing setae.

Moliniform antennae. Every intact antenna in the six type specimens has 32 antennomeres; from 0.5 to 0.7 times longer than body in larger and smaller adults, respectively. First antennomere four times shorter than second antennomere, and apical antennomere 1.3 longer than wide (Fig. 1); the other antennomeres, as long as wide (Fig. 7).

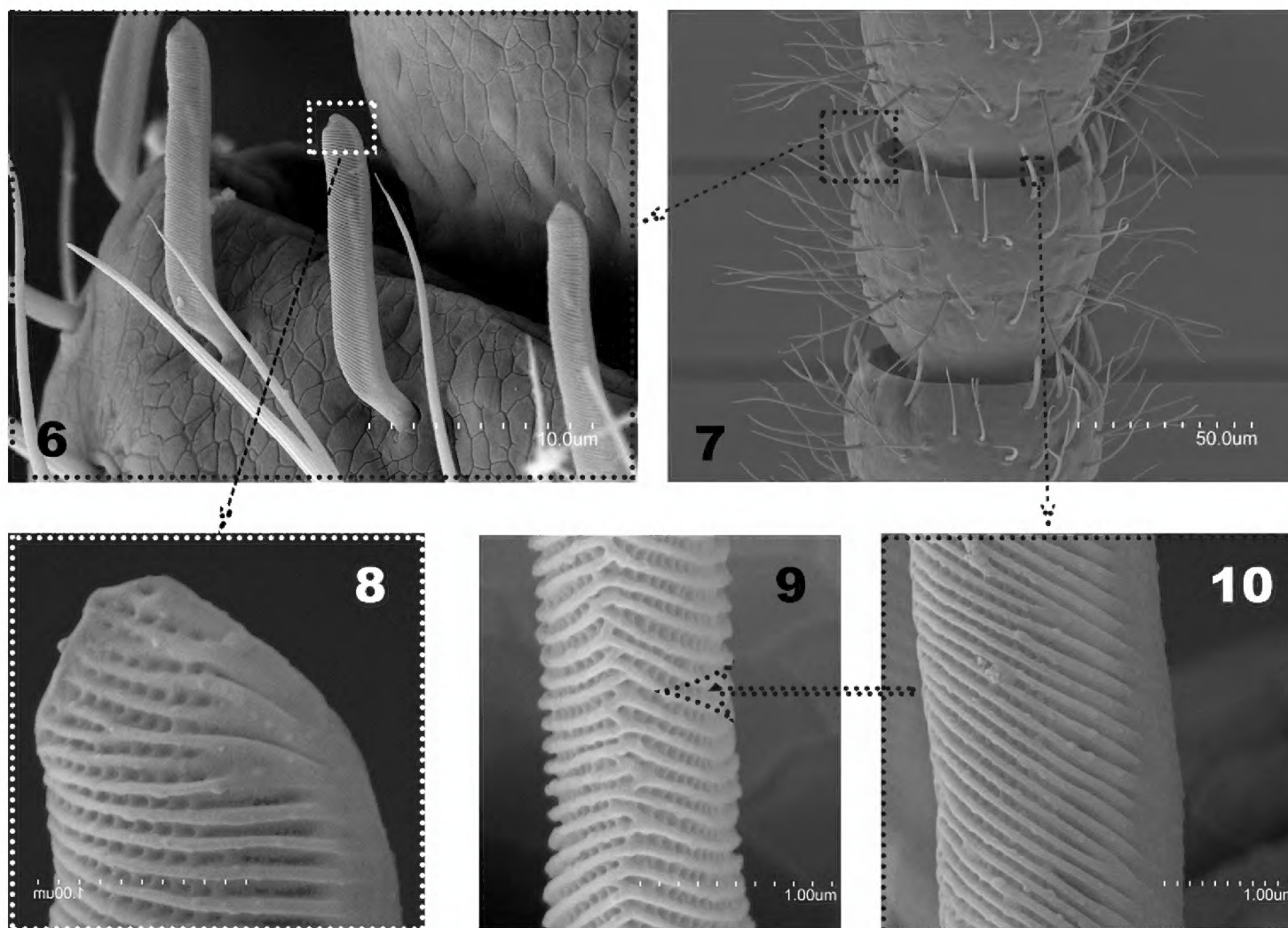


**Figures 1–5.** *Haplocampa wagnelli* Sendra, sp. n. **1** last and penultimate antennomere **2** olfactory chemoreceptors within the cupuliform organ **3** detail of olfactory chemoreceptor, paratype **4** coniform sensilla on the last antennomeres **5** two *rosette* sensilla in the last antennomere.

Cupuliform organ occupying 1/3 of the total length of the apical antennomere with about five complex olfactory chemoreceptors, each one a multiperforated–folded spiral structure, all tightly packed in the narrow open space of the cupuliform organ (Figs 2, 3). Distal and central antennomeres with a sensorial equipment: one whorl of bifurcated macrosetae, two to three whorls of untidy setae, and a single distal whorl of 10–13 short and thick *gouge* sensilla of 14–16  $\mu\text{m}$  long 2–3 very short grooved closed–bud form sensilla 6–8  $\mu\text{m}$  long; this sensorial equipment is also present in the apical antennomere (Figs 4, 6–10). Proximal antennomeres with typical trichobothria plus a thick and long sensillum on the third antennomere, located in ventral position, although the ventral *c* and *d* macrosetae are not differentiated.

Head subtrapezoidal with slightly protuberant lateral posterior angles (Fig. 11). Plain frontal process with the slightly differenced frontal smooth macrosetae (Fig. 12). From the three macrosetae along each side of the line of insertion of antennomere and *x* setae, *a* macrosetae is not differentiated and *i/p/x* have 36/57/23 relative lengths, all smooth (Fig. 12). Suboval labial palps with latero-external long thick sensillum, with two guard setae, up to 8 setae on anterior border and up to 80 neuroglandular setae.

Thoracic macrosetae distribution (Fig. 13): pronotum with 1+1 *ma*, 1+1 *la*, 1+1 *lp*; mesonotum with 1+1 *ma*, 1+1 *la*, 2+2 *lp*<sub>2,3</sub>; metanotum with 1+1 *ma*, 1+1 *lp*<sub>2</sub> macrosetae. All macrosetae relatively well developed, long with thin long barbs; marginal setae slightly longer and thicker than clothing setae and also smooth. Legs very slightly elon-



**Figures 6–10.** *Haplocampa wagnelli* Sendra, sp. n. **6** distal gouge sensilla whorl in a medial antennomere **7** medial antennomere **8** detail of the ending portion of a gouge sensillum **9** detail of external side of a gouge sensillum **10** detail of lateral side of a gouge sensillum.

gated, metathoracic legs reaching the VIII abdominal segment in smaller adults and the VI in larger ones. Femur and tibia similar in length but tarsus clearly shorter and thicker (tibia/tarsus ratio 0.6 to 0.7) (Table 1). Femur I–III with one dorsal macrosetae well differentiated with a few thin long barbs in its distal half. Calcars with a few thin, long barbs throughout. Tibia I–III with two or three ventral macrosetae bifurcated in the apex (Fig. 17). Three or two dorsal, lateral and sometimes ventral tarsal setae similar to clothing setae but much longer (Fig. 18). Unequal claws (posterior claw 1.5 longer than anterior) with large lateral crests and no lateral process; ventral side of the claws noticeably ridged and covered by a micro-granulation surface; a spiny protrusion is visible in the basal portion of both claws (Figs 18–21); posterior claw with a large backward overhang (Figs 18, 19).

Distribution of abdominal macrosetae on urotergites (Fig. 22): 1+1 *ma* on I–III; 1+1 *ma*, 1+1 *lp*<sub>2</sub> on IV; 1+1 *ma*, 1+1 *la* and 2+2 *lp*<sub>2,3</sub> on V–VII; 1+1 *ma* and 3+3 *lp*<sub>1,2,3</sub> on VIII; 1+1 *ma* (slightly backwards) and 5+5 *lp*<sub>1,2,3,4,5</sub> on IX abdominal segment. All tergal abdominal macrosetae long and well differentiated with thin barbs along the half to third distal.

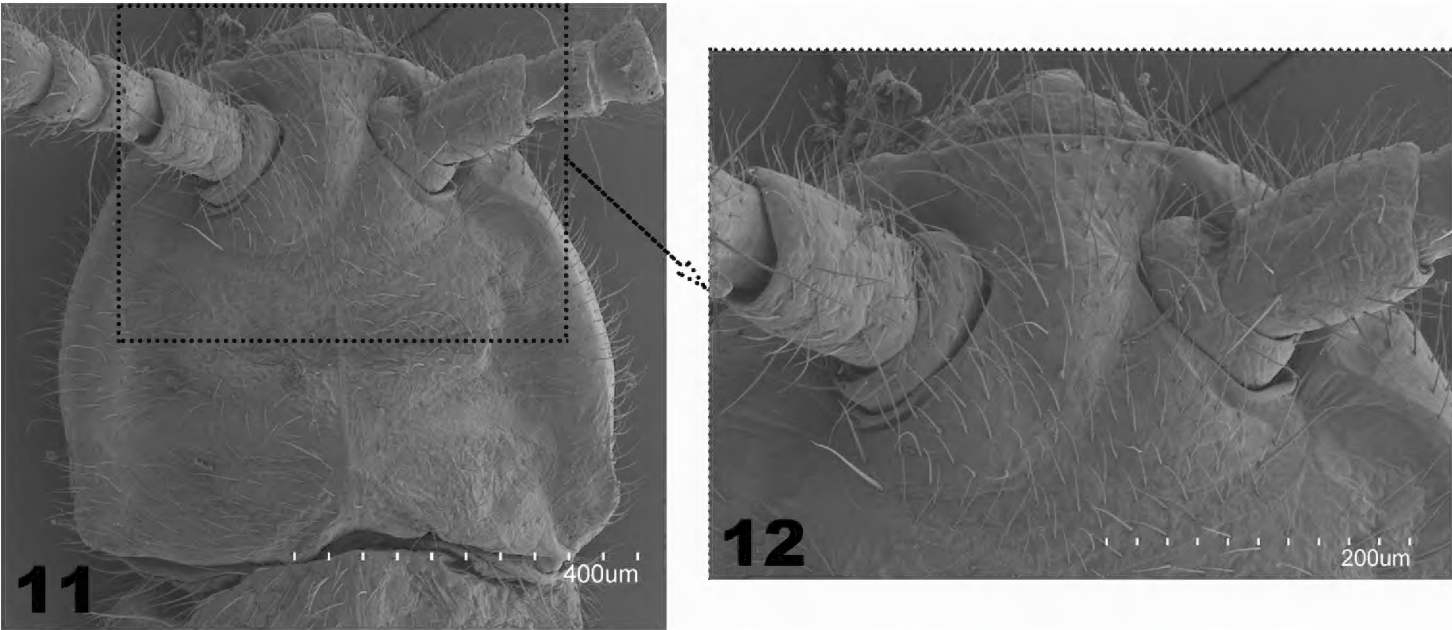
Urosternite I with 6+6 macrosetae (Figs 23–24); II to VII with 4+4 macrosetae; VIII with 1+1 macrosetae; short to middle size urosternal macrosetae, bi or trifurcated or with long barbs. Short styli with smooth short apical setae with two long teeth;

**Table 1.** *Haplocampa wagnelli* Sendra, sp. n., length of the body, antennae and metathoracic leg including their segments, the cerci (units in mm), and the number of antennomeres.

Specimen	Body length	Antennomeres	Antennae length	Segment length of a metathoracic leg						Total metathoracic length
				Coxa	Trochanter	Femur	Tibia	Tarsus	Pretarsus	
Paratype, ♀04	3.40	32	2.50	0.21	0.18	0.45	0.41	0.27	0.10	1.62
Paratype, ♀05	3.75	32	2.35	0.20	0.12	0.43	0.40	0.28	0.85	1.47
Paratype, ♂01	4.40	32	2.52	0.21	0.12	0.48	0.46	0.28	0.10	1.65
Paratype, ♀02	4.90	32	2.65	0.22	0.18	0.51	0.48	0.29	0.11	1.78
Paratype, ♀03	5.05	32	3.05	0.25	0.22	0.60	0.55	0.35	0.10	2.07
Holotype, ♀01	6.02	32	3.20	0.21	0.17	0.48	0.46	0.28	0.11	2.15

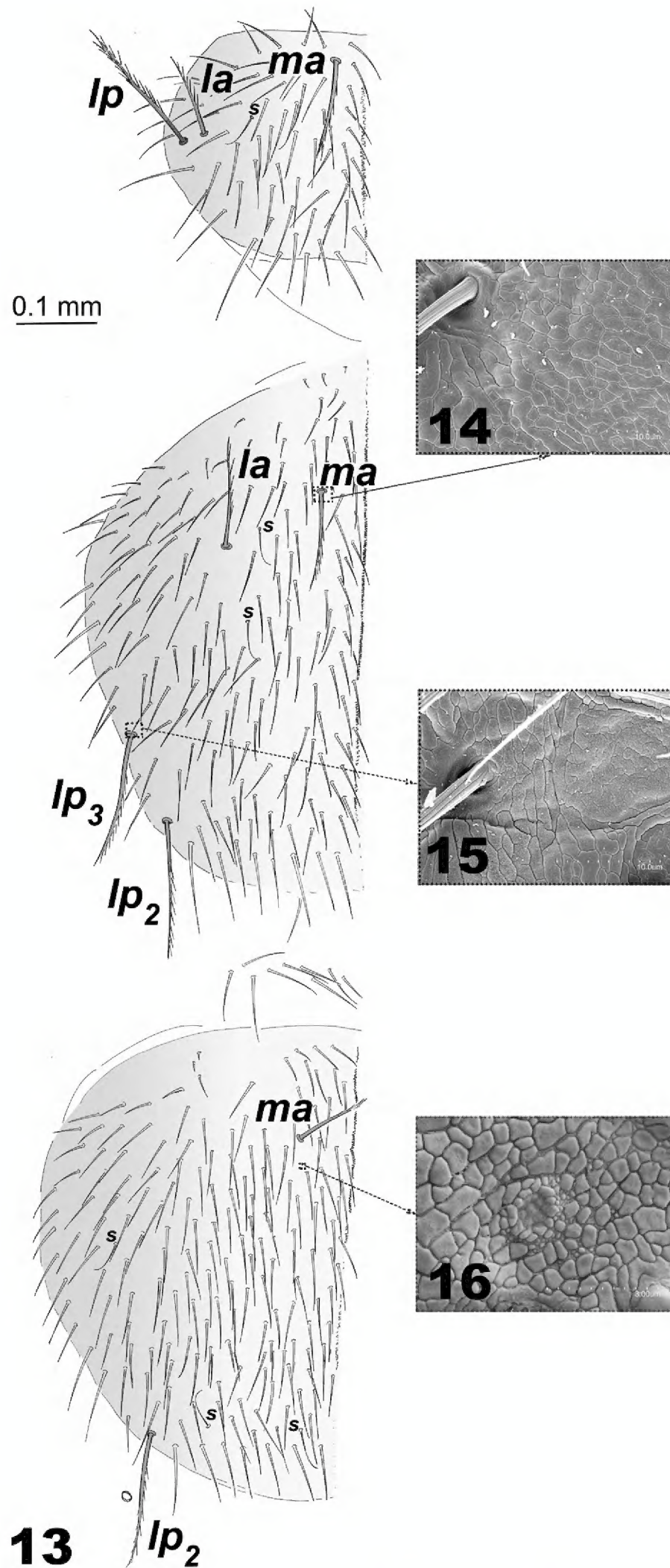
**Table 2.** *Haplocampa wagnelli* Sendra, sp. n., length of cercal articles and total length (units in mm) including number of articles of each cercus.

Specimen, body length	Cerci, Articles length							
	Base (secondary article)	1 <sup>st</sup>	2 <sup>nd</sup>	3 <sup>rd</sup>	4 <sup>th</sup>	5 <sup>th</sup>	6 <sup>th</sup>	Total length
Paratype ♀04, 3.40 mm	0.78 (7)	0.22	0.25	0.28	0.36	0.38	-	2.26
Paratype ♀05, 3.75 mm	0.70 (8)	0.22	0.30	0.38	0.40	0.42	-	2.42
Paratype ♂01, 4.4 mm	0.35 (3)	0.18	0.25	0.28	0.30	0.40	0.42	2.18
Paratype ♀02, 4.9 mm	0.62 (4)	0.21	0.24	0.26	0.31	0.39	0.44	2.48
Paratype ♀03, 5.05	0.92 (7)	0.25	0.28	0.30	0.32	0.38	0.35	2.70
Holotype ♀01, 6.02 mm	0.88 (6)	0.25	0.30	0.32	0.35	0.38	0.38	2.85

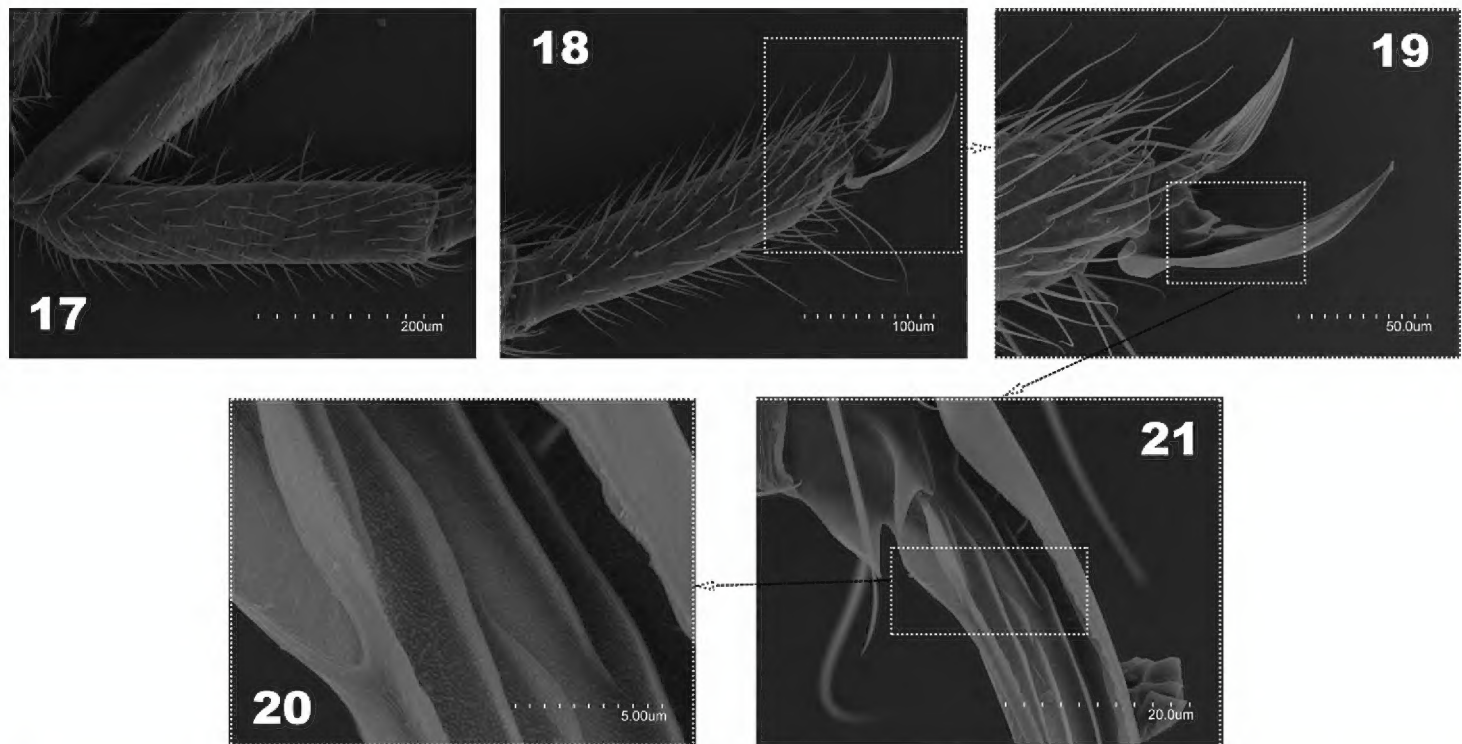


**Figures 11, 12.** *Haplocampa wagnelli* Sendra, sp. n. **11** dorsal side of the head **12** frontal process.

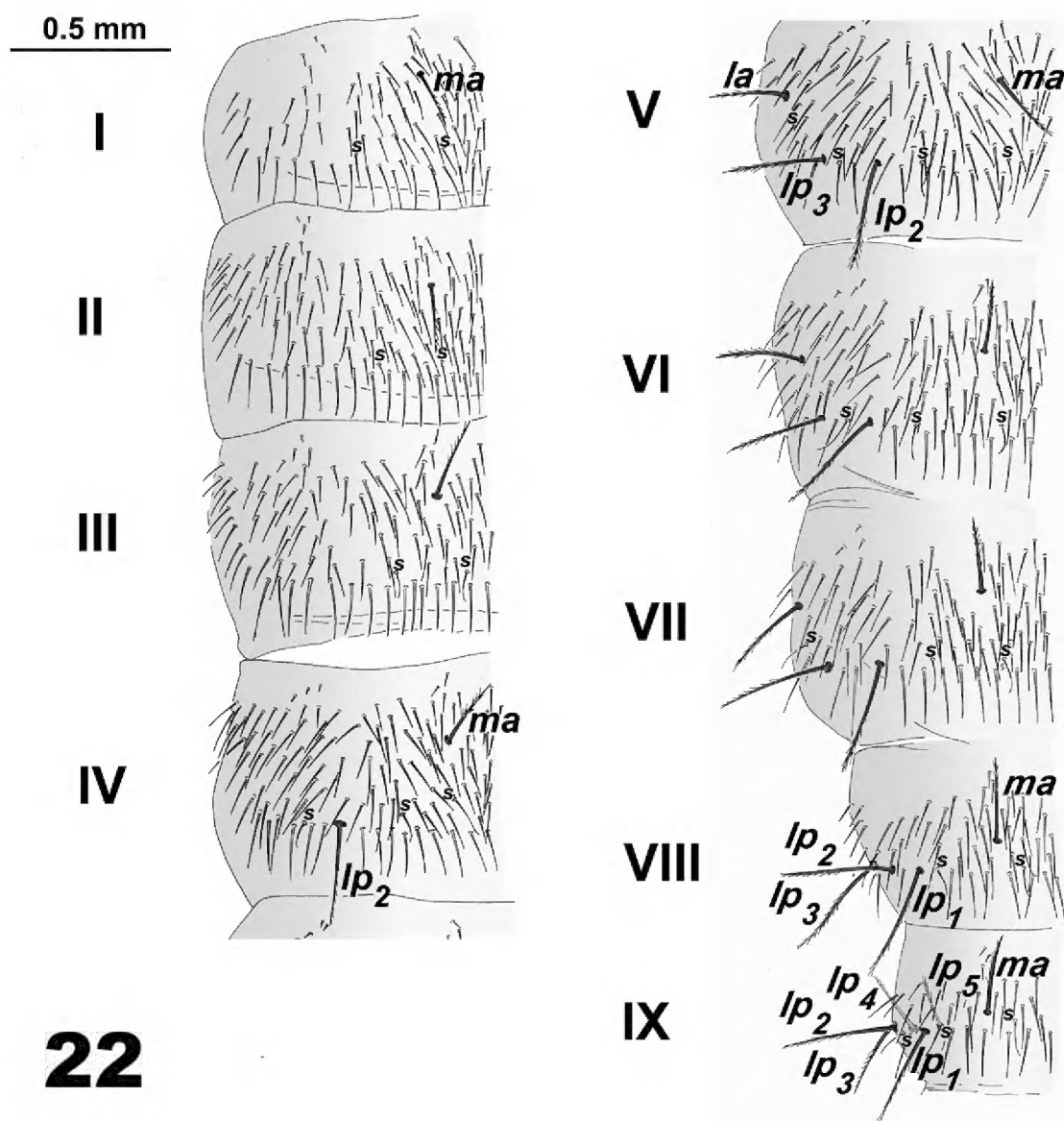
bifurcated subapical and ventromedial setae (Fig. 25). Cerci half shorter than the body length, from 0.64× in the smaller adults to 0.47× in the holotype; so, the length of the cerci increases disproportionally with the body size. As well, the length of the articles increases from proximal to distal. Basal article is divided into three to eight secondary articles, followed by five to six primary articles bearing from two to five whorls of



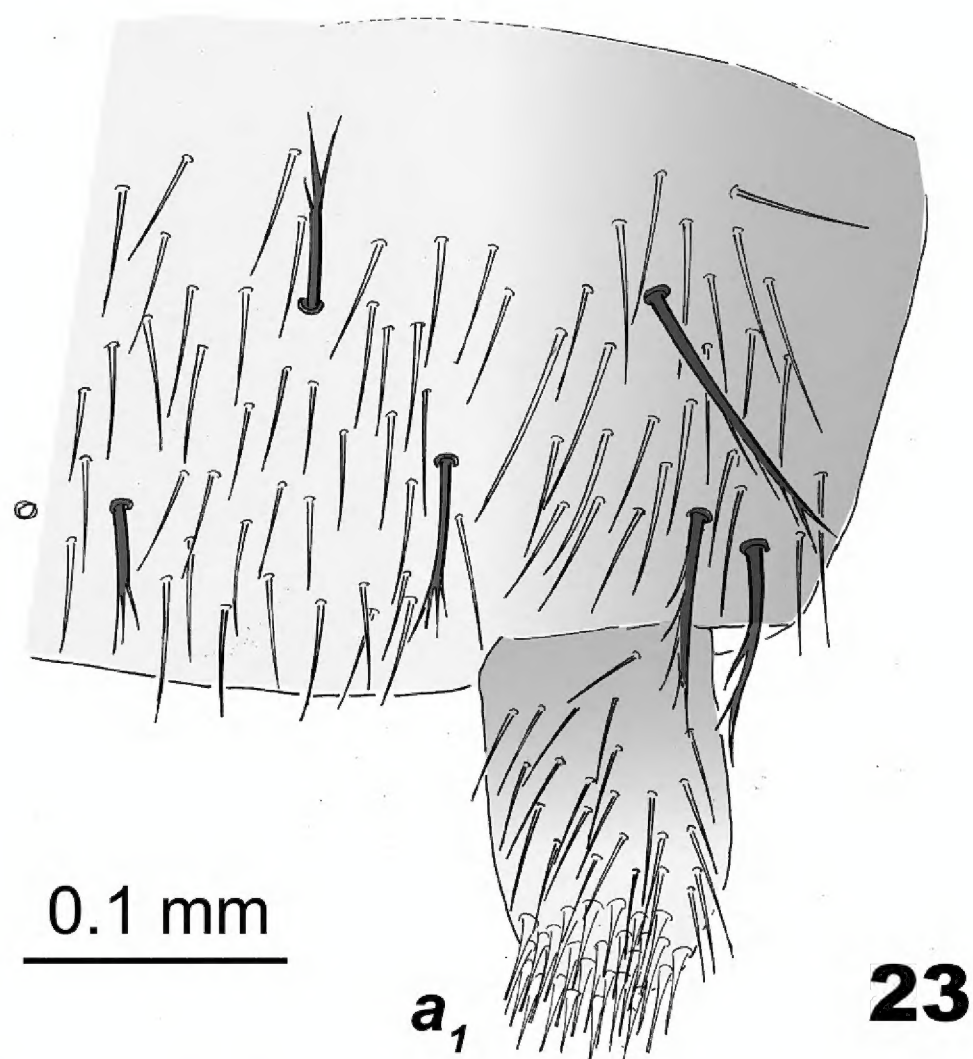
**Figures 13–16.** *Haplocampa wagnelli* Sendra, sp. n. **13** pro-, meso- and metanotum, left side, holotype **14** detail of epicuticle surface on mesonotum **15** detail of epicuticle surface on mesonotum **16** detail of epicuticle surface on metanotum including external gland.



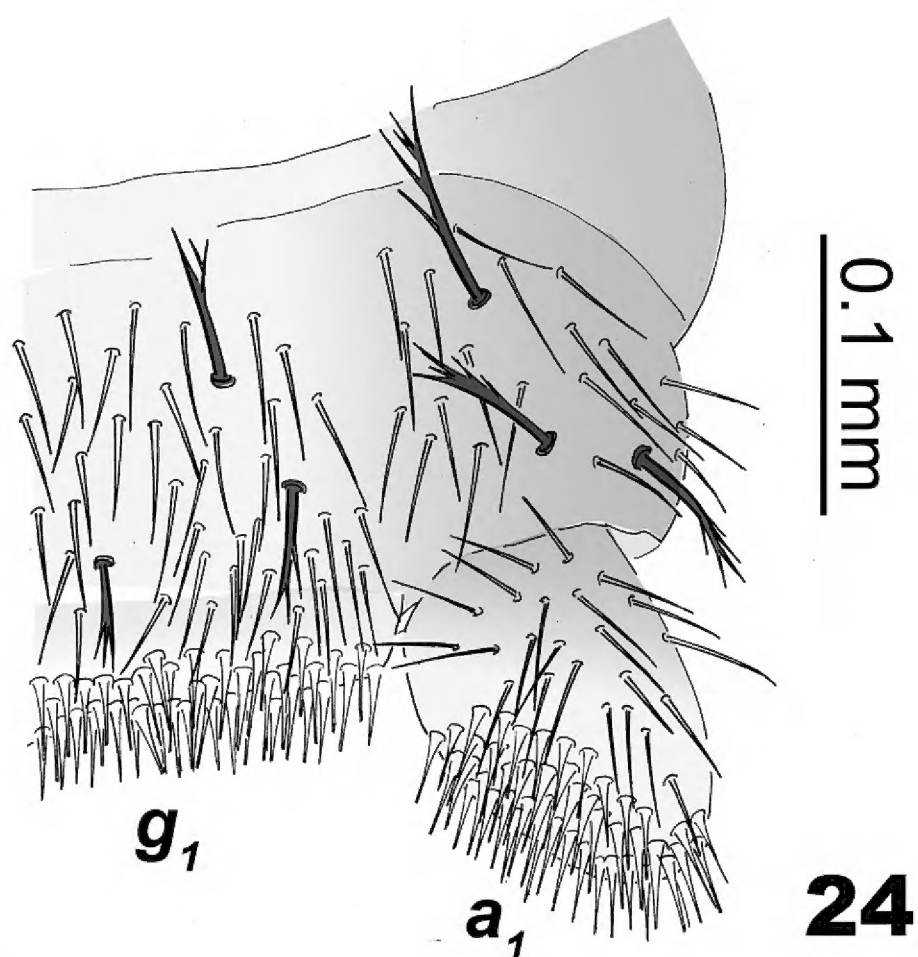
**Figures 17–21.** *Haplocampa wagnelli* Sendra, sp. n. **17** distal portion of femur and tibia from a metathoracic leg **18** tarsus **19** end of the tarsus and telotarsus **20** detail of posterior claw, lateral side **21** detail of posterior claw, lateral side.



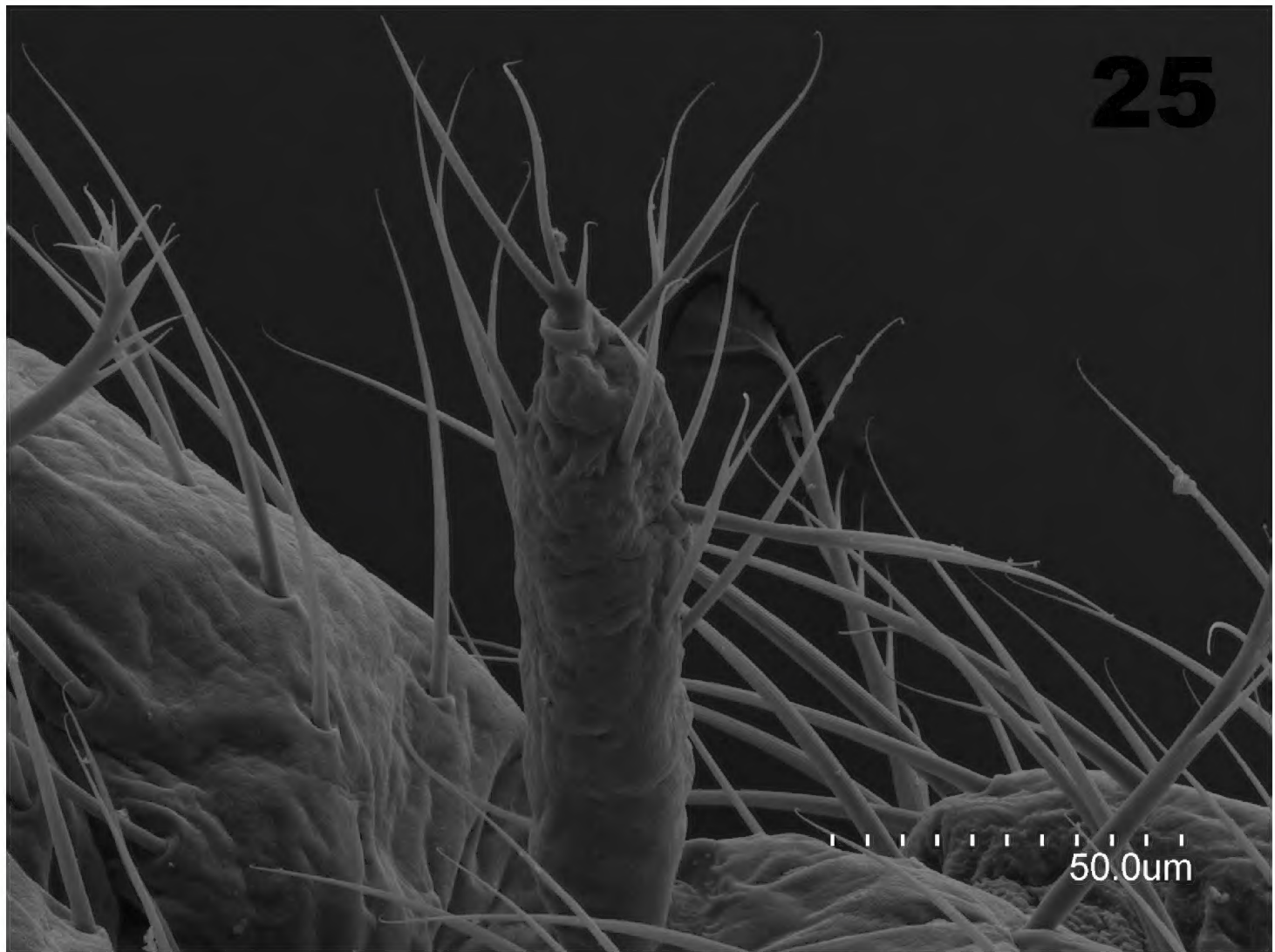
**Figure 22.** *Haplocampa wagnelli* Sendra, sp. n. Urotergites I–IX, left side, holotype.



**Figure 23.** *Haplocampa wagnelli* Sendra, sp. n. First female urosternite, ♀ paratype, 6 mm.



**Figure 24.** *Haplocampa wagnelli* Sendra, sp. n. First male urosternite, ♂ paratype, 4.4 mm.



**Figure 25.** *Haplocampa wagnelli* Sendra, sp. n. Left stylus of the sixth urosternite.

bifurcated macrosetae, and three to six smooth setae including the distal setae whorl in each primary article (Table 2; Figs 26, 27).

Female urosternite I with short subcylindrical appendages, each bearing up to 30  $a_1$ -glandular setae in a distal field (Fig. 23).

Male urosternite I with short moderately thick subcylindrical appendages, each bearing about 50  $a_1$ -glandular setae in a large field; up to setae covered the with two to three rows the posterior part of the first urosternite (Fig. 24).

**Remarks.** The most visible features are the slightly troglomorphic characteristics of *H. wagnelli* sp. n., as shown by its antennae with 32 antennomeres, a record within the genus *Haplocampa* but a moderate antennomere number in a troglomorphic campodeid; and the five complex olfactory chemoreceptors, each one a multiperforated, folded-spiral structure. However, any comparison with other *Haplocampa* species is currently impossible since these sensilla have not been described in any other species of the genus. The closest species to *H. wagnelli* sp. n. is *H. rugglesi* from Mount Rainier (Washington, USA), with equal macrosetae distribution on nota and similar on urotergites. Nevertheless, some taxonomic features are unique to *H. wagnelli* sp. n., such as medial anterior macrosetae on urotergites and three tibial ventral macrosetae. Many taxonomical details remain incomparable what is known described species, due to the lack of high magnifications.



**Figure 26.** *Haplocampa wagnelli* Sendra, sp. n. First primary cercal article, lateral side.



**Figure 27.** *Haplocampa wagnelli* Sendra, sp. n. Last primary cercal article.

## Discussion

### An attempt at *Haplocampa* redescription with a key to species

Silvestri (1911) described the genus, and Paclt (1957) redescribed it. By following these taxonomical criteria and adding a few others, it is worth attempting a new description of *Haplocampa*:

Antennae with moniliform antennomeres and short cerci with a few primary articles. Subtrapezoidal head slightly enlarged in the posterior lateral side. Medial anterior (1+1), lateral anterior (1+1) and lateral posterior (1+1) macrosetae on pronotum; medial anterior (1+1), lateral anterior (1+1) and lateral posterior (2+2) on mesonotum; and medial anterior (1+1) and lateral posterior (1+1-2+2) on metanotum. Dorso-femoral macrosetae one. One to three tibial-ventral macrosetae. Tarsus short and enlarged. Unequal claws with large lateral crests and no lateral process; basal portion of both claws with a visible spiny protrusion; posterior claw with a large backward overhang. Medial anterior or medial posterior urotergal macrosetae present; with or without lateral anterior urotergal macrosetae; and, lateral posterior urotergal macrosetae 0, 1 ( $lp_2$ ) or 2 ( $lp_{2,3}$ ) on urotergites V to VII. Urosternite I with 6+6 macrosetae; urosternites II to VII with 4+4 macrosetae; urosternite VIII with 1+1. Plain stylus with smooth or a few tiny barbs on stylus setae. Male with glandular  $a_1$  and  $g_1$ -setae. Female with glandular  $a_1$ -setae.

### *Haplocampa* species taxonomical key

- 1 Lateral posterior macrosetae 2+2 on metanotum; without lateral anterior macrosetae on urotergites; antennae with 24–26 antennomeres.....*Haplocampa drakei*
- Lateral posterior macrosetae 1+1 on metanotum; with lateral anterior macrosetae 1+1 on urotergites .....2
- 2 Without posterior macrosetae on first and second urotergites; antennae with 20 antennomeres ..... *Haplocampa chapmani*
- Medial anterior or medial posterior macrosetae 1+1 on first and second urotergites.....3
- 3 Medial posterior macrosetae 1+1 on first and second urotergites; two tibial ventral macrosetae..... *Haplocampa* cf. *chapmani*
- Medial anterior macrosetae 1+1 on first and second urotergite.....4
- 4 Medial anterior macrosetae 1+1 on third to seventh urotergites; two or three tibial ventral macrosetae; antennae with 32 antennomeres .....  
.....*Haplocampa wagnelli* sp. n.
- Medial anterior macrosetae only on first urotergites; one tibial ventral macrosetae; antennae up to 21 antennomeres.....5
- 5 Lateral posterior macrosetae 1+1 on third urotergite; antennae with 19–21 antennomeres .....*Haplocampa wheeleri*
- Without lateral posterior macrosetae on third urotergite; antennae with 21 antennomeres .....*Haplocampa rugglesi*

## Description of type localities (caves)

The caves are all located near the town of Port Alberni, Vancouver Island, British Columbia, Canada (Figs 28–33). The limestone area covers roughly 2400 hectares, and within that area lay over 20 hidden caves, as well as many resurgences, dry sinks, small pits and fissures. Only a short drive and an easy hike are required to reach most caves, providing great opportunities to turn this area into an outstanding caving recreational site if properly managed.

### Fossli slot caves

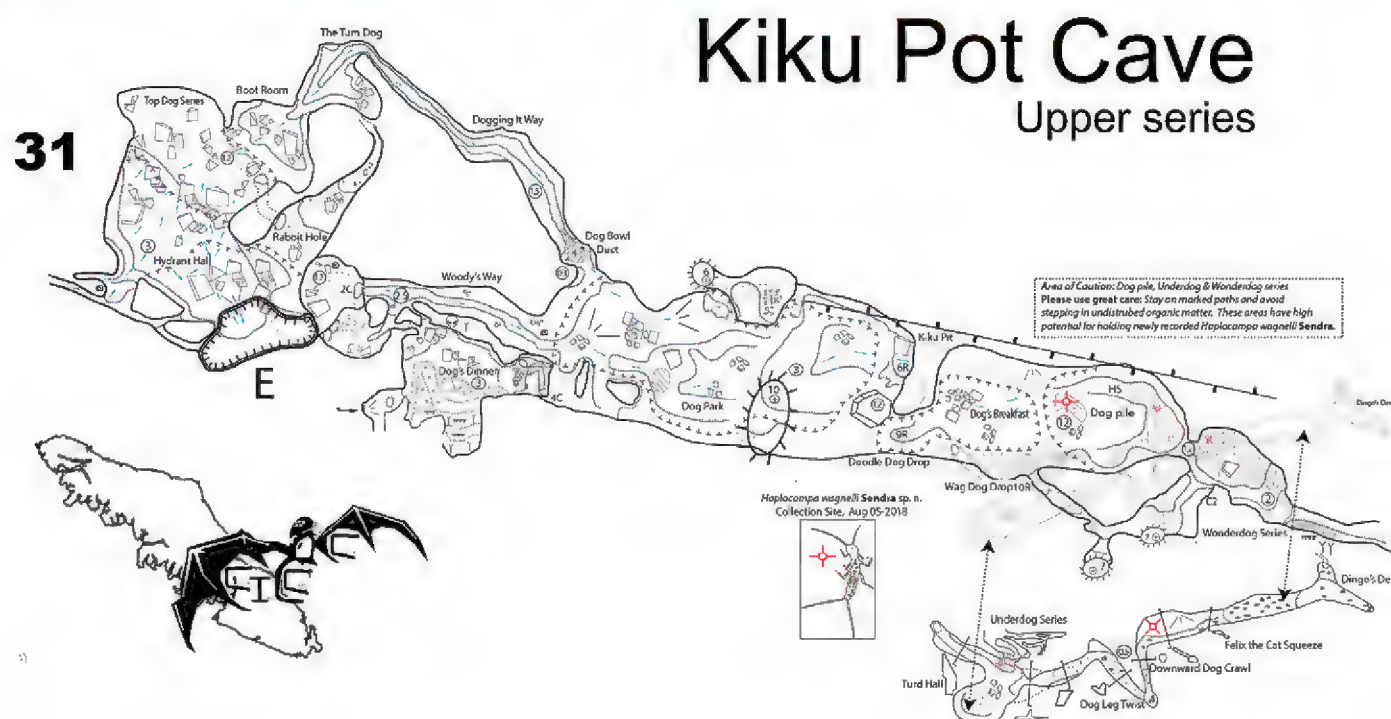
Fossli #1 (L63.5 D25): swallet entrance with active surface stream. First sightings of *H. wagnelli* sp. n. on 5<sup>th</sup> April 2005.

Fossli #2 (L67.5 D26.5): small slot entrance filled with rotten wood. Upper samples collected 15<sup>th</sup> July 2018, 30 m from the entrance in a moist bed of sandy organic debris. Lower samples collected 6<sup>th</sup> August 2018, 60 m from the entrance in a moist bed of sandy organic debris 2 m above sump. *H. wagnelli* sp. n. mud workings visible at both sites.

Kiku Pot cave, (L1489 D92): Breakdown entrance with active stream passage through-out system. *H. wagnelli* sp. n. first sightings August 2017 while surveying. Collection taken 5<sup>th</sup> August 2018, at bottom waterfall just below where water disappears approximately 150 m from the entrance on a medium. A medium sized bed of sandy organic material with scattered woody debris. *H. wagnelli* sp. n. workings were visible over 75%. Area floods during high water. Many mud workings visible on muddy shelves higher in passage. At the time of collection, an adult fungus gnat was noticed hopping around.



**Figure 28.** Map of western of North-America, highlighting in red the limestone area near Port Alberni (Vancouver Island, Canada) where Fossli Slots and Kiku Pots caves are located.



**Figures 29–33.** **29** Map of Fossli Slots caves with spots where *Haplocampa wagnelli* sp. n. was seen **30** entrance of Fossli Slot #2 cave **31** Kiku Pot cave with spots where *Haplocampa wagnelli* sp. n. was seen **32** entrance of Kiku Pot cave with Felix Ossigi-Bonanno and Craig Wagnell after the success finding **33** entrance of Kiku Pot cave viewed from inside the cave.

### Cave Conservation Vancouver Island

Vancouver Island is known to have over 1600 caves, with more mapped and explored caves than the rest of Canada combined. Some caves reach over 10 km, and some host unique geological, palaeontological, archaeological and biological features. Vancouver Island caves are mostly active caves, with streams and rivers running through them most of the year. The caves help the streams to maintain constant water temperatures year round and a proper pH, which increases water quality for fish and wildlife. So far, little has been done to protect the caves from poor logging, mining and recreational practices. All caves west of the Port Alberni area are easily accessed by the public and none so far have protection or proper management. Unfortunately, some already have seen misuse. More needs to be done in the future if we want to protect this special resource.

### Phylogenetic affinities of the genus *Haplocampa* with notable biospeleological and biogeographical comments

In *Haplocampa* species, their unequal claws have large lateral crests, as do many genera of Plusiocampinae. Applying the right criteria, Paclt (1957) included *Haplocampa* within Campodeinae. In fact, many taxonomical features of *Haplocampa* are held by Campodeinae, such as the distribution and number of pronotum macrosetae, with at most 3+3 medial anterior, lateral anterior and lateral posterior macrosetae. Other notable features of *Haplocampa* are shared with many Campodeinae genera, namely, epicuticle with rosette gland formations; plain frontal process; number and distribution of urotergal macrosetae with medial macrosetae and a maximum of three pairs of lateral posterior macrosetae; simple stylus setae; and number and distribution of urosternal macrosetae, with up to eight pairs of macrosetae on first the urosternite, up to five pairs of macrosetae on the second to seventh urosternites and one pair on the eighth.

In all likelihood, *Pacificampa* Chevrizov, 1978 is the most closely related to *Haplocampa*, given the strong similarities in the number and distribution of the macrosetae body and the absence of lateral pretarsus processes, with one important difference: the lack of lateral crests in *Pacificampa* (Chevrizov 1978; Sendra et al. 2018). The same differential feature is shown by other related genera of *Haplocampa*, in *Metriocampa* Silvestri, 1912 and *Eumesocampa* Silvestri, 1933. All these four genera can be found in the East of Asia and in North America, on both sides of the northern Pacific Ocean, which suggests dispersal events over the Bering Land Bridge. This hypothetical palaeobiogeographical distribution was suggested by Ferguson (1997) for *Eumesocampa*, *Haplocampa*, *Pacificampa* and *Plutocampa* Chevrizov, 1978. Another perhaps more parsimonious hypothesis could be that they had an ancient Laurasian distribution and their current distribution reflects a vicariance event after the breacking of the Bering Bridge (Loris Galli pers. suggestion).

*Haplocampa* and *Pacificampa* share ecological similarities, and phylogenetic, too. Both are present in subterranean ecosystems. In the case of *Pacificampa*, all of the five known species have been found in caves and can be considered troglobites. Three of these species can be found in the north of the Korean Peninsula (Chevrizov 1978; Ferguson 1997) and two were recently described in two southern Japanese Islands (Sendra et al. 2018). In *Haplocampa*, the five described species have been found within the soil at high-altitude localities. However, Ferguson (1981) suggested no less than eight undescribed species of *Haplocampa* from caves located in the Ozarks karstic region at the centre of North America and in the small volcanic and karstic areas of the Pacific coast. Ferguson (1981) remarked that in the case of *Haplocampa*, *Eumesocampa* and *Tricampa* Silvestri, 1933, 'All three have epigeal members at high latitudes or high altitudes in the western mountains, and cavernicolous members at lower latitudes and altitudes'. Nevertheless, *Haplocampa wagnelli* sp. n. is an exception to Ferguson's comment (1981).

*H. wagnelli* sp. n. is a slight troglomorphic species and several features show this. Among these features are the very slight elongation of antennae,  $0.5\times$  to  $0.7\times$  the body length, with moniliform antennomeres, and the cerci  $0.5\times$  to  $0.6\times$  the body length. In troglomorphic campodeids, the length of antennae can double that of the body, with always more than 30 antennomeres, and the cerci can be two or three times the body length; there is also an increase in the number of the cercal articles. Furthermore, troglotic campodeids have elongated legs, reaching the end of the abdomen and a slim body. All of these features are trademarks of highly adapted subterranean campodeid species (Sendra et al. 2017). However, in *H. wagnelli* sp. n., its legs reach the VI to VIII abdominal segment and the body is not slender. But the trogliont condition of *H. wagnelli* is supported by the presence of 32 antennomeres, five complex, multi-perforated, folded-spiral sensilla, and a high number (14–16) of thick gouge sensilla. These are solid evidences for subterranean adaptations. For these reasons, *H. wagnelli* sp. n. can be considered to be a slightly trogliont species adapted to live in caves and other subterranean spaces, but it could probably also be found in soil habitats. This is the case for the soil-dwelling species *H. drakei*, with 26 antennomeres, found nearby in Banff National Park, Alberta, Canada (Silvestri 1933).

*H. wagnelli* sp. n. may represent one of the most northerly cave-dwelling adapted dipluran species being found at  $49^\circ$  latitude north. The most northerly cave-dwelling species is *Litocampa hubarti* Bareth, 1999, found in Grotte Lyell (Liège, Belgium) at  $50^\circ$  latitude north, and like *H. wagnelli* sp. n., it shows humble morphological subterranean-adapted features (Bareth 1999). Both species are geographically in the limits of the Last Glacial Maximum. Furthermore, in the case of *H. wagnelli* sp. n., its current distributional area was under the Cordilleran Ice Sheet the Late Wisconsinian North American ice sheet complex, during the Last Glacial Maximum 18 ka BP (Dyke 2004). Several hundred years later the retreat of the glacial ice occurred, and as a consequence, the subterranean habitat colonisation of Vancouver Island was possible.

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## References

- Bareth C (1999) Une nouvelle espèce de *Litocampa* découverte dans une grotte de Belgique (Diploures Campodeidae). Bulletin des Chercheurs de la Wallonie 39: 9–13.
- Bareth C, Condé B (1981) Nouveaux Campodéidés de grottes d’Espagne. Revue suisse de Zoologie 88(3): 775–786. <https://doi.org/10.5962/bhl.part.82407>
- Bareth C, Juberthie-Jupeau L (1996) Ultrastructure of the formations of the cuticle of *Campodea kervillei* Denis (Insecta: Diplura). Bulletin des Académie & Société Lorraines des Sciences 35(4): 231–241.
- Chevrizov BP (1978) Two new genera of the family Campodeidae from the Far East caves. Zoologicheskij Zhurnal 57(2): 197–205. [In Russian, with English summary]
- Condé B (1949) Campodéidés cavernicoles de la région des Appalaches. Notes Biospéologiques 4: 125–137.
- Condé B (1956) Matériaux pour une Monographie des Diploures Campodéidés. Mémoires du Muséum National d’Histoire naturelle Série A. Zoologie 12: 1–202.
- Condé B, Bareth C (1996) Une nouvelle espèce de *Litocampa* de grottes de l’état de Virginie (Diplura, Campodeidae). Mémoires de Biospéologie 23: 143–147.
- Condé B, Geeraert P (1962) Campodéidés endogés du centre des États-Unis. Archives de Zoologie expérimentale et Générale 101(8): 73–160.
- Dyke SA (2004) An outline of North American deglaciation with emphasis on central and northern Canada. Quaternary Glaciations-Extent and Chronology - Part II: North America. Developments in Quaternary Sciences 2: 373–424. [https://doi.org/10.1016/s1571-0866\(04\)80209-4](https://doi.org/10.1016/s1571-0866(04)80209-4)
- Elliott WR, Reddell JP, Craig Rudolph D, Graening GO, Briggs TS, Ubick D, Aalbu RL, Krejca J, Taylor SJ (2017) The Cave Fauna of California Vol. 64, Supplement 1. Proceedings of the California Academy of Sciences. 311 pp. [25 tables, 9 maps, 4 graphs, 105 photos]

- Ferguson LM (1981) Cave Diplura of the United States. Proceedings of the Eighth International Congress of Speleology, Kentucky: 11–12.
- Ferguson LM (1992) Diplura of Lava Tube Caves. Proceedings of the 6th International Symposium on Vulcacospeleology, Hilo Hawaii, 281–284.
- Ferguson LM (1996) *Condeicampa langei*, new genus and species of Dipluran (Diplura: Campodeidae) from Whipple Cave, Nevada, USA. Mémoires de Biospéologie XXIII: 133–141.
- Ferguson LM (1997) A report on a new species of *Pacificampa* (Diplura: Campodeidae) from a cave in China and comparison of some North American genera to *Pacificampa* and *Plutocampa* previously only known from the Far East of Russia. Proceedings of the 12th International Congress of Speleology, La Chaux-de-Fonds, Neuchâtel, Switzerland 3: 315–317.
- Ferguson LM (2009) Preliminary report on the cave diplura of Colorado (Hexapoda: Diplura: Campodeidae). In: White WB (Ed.) Proceedings of the 15<sup>th</sup> International Congress of Speleology, Kerrville, Texas. Vol. 3. Contributed Papers, 1283–1285.
- Graening GO, Shcherbanyuk Y, Arghandiwa M (2014) Annotated Checklist of the Diplura (Hexapoda: Entognatha) of California. Zootaxa 3780(2): 297–322. <https://doi.org/10.11646/zootaxa.3780.2.5>
- Paclt J (1957) Diplura. In: Genera Insectorum. P. Wytsman, 212° fasc, 1–123.
- Packard AS (1871) The Mammoth Cave and its inhabitants: On the Crustaceans and Insects. The American Naturalist 5: 744. <https://doi.org/10.1086/270866>
- Sendra A, Palacios J, García A, Montejó M (2016) New Species of Campodeidae (Diplura) from Mexican caves. Zootaxa 4072(5): 540–558. <https://doi.org/10.11646/zootaxa.4072.5.2>
- Sendra A, Jiménez-Valverde A, Rochat J, Legros V, Gasnier S, Cazanove G (2017) A new and remarkable troglobitic *Lepidocampa* Oudemans, 1890 species from La Réunion Island, with a discussion on troglobiomorphic adaptations in campodeids (Diplura). Zoologischer Anzeiger 266: 95–104. <https://doi.org/10.1016/j.jcz.2016.11.005>
- Sendra A, Yoshizawa K, Lopes-Ferreira R (2018) New oversize troglobitic species of Campodeidae in Japan (Diplura). Subterranean Biology 27: 53–73. <https://doi.org/10.3897/subtbiol.27.28575>
- Silvestri F (1911) Nuovi Generi e Nuove Spezie di Campodeidae (Thysanura) dell’America settentrionale. Bolletino del Laboratori di Zoologia generale e agraria della R. Scuola superiore d’Agricoltura in Portici 6: 7–25.
- Silvestri F (1933) Quarto Contributo alla conoscenza dei Campodeidae (Thysanura) del Nord America. Bolletino del Laboratori di Zoologia Generale ed Agraria del R. Istituto Superiore Agrario di Portici 27: 156–204.
- Wygodzinsky P (1944) Contribuição ao conhecimento da familia Campodeidae (Entotrophi, Insecta) do Mexico. Anales de la Escuela Nacional de Ciencias Biológicas 3: 367–404.

## **Supplementary material I**

### **A video shot by Felix Ossig-Bonanno (2017) from Fossli Slots Caves**

Authors: Alberto Sendra, Craig Wagnell

Data type: multimedia

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